

REVISION OF THE GENUS *PARADA* HORVÁTH (HEMIPTERA: TINGIDAE)
WITH CLADISTIC ANALYSIS

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Abstract.—Three new species of *Parada* from New Caledonia are described: *P. minuta*, *P. paitae* and *P. majuscula*. The monotypic *Alloeocysta approba* Drake is considered a junior synonym of *Parada* and to which its only included species is transferred. The evolution of certain characters, and the relationships among species of *Parada* are presented together with a cladistic analysis. An identification key for these species is also given.

Key Words: *Parada*, Tingidae, new species, evolution, phylogeny, key

Horváth (1925) erected *Parada* as a subgenus of *Cysteochila* Stål for the reception of *Cysteochila (Parada) taeniophora* Horváth (1925). *Cysteochila* has the paranota widely reflected, inflated, covering the lateral carinae, and the internal margins (« margine interno ») rounded, while *Parada* has the paranota narrowly reflexed, superficially adpressed onto the pronotum and not covering the lateral carinae, and the internal margins slightly sinuate and never rounded (Horváth 1925). Drake (1942) raised *Parada* to generic level, and add two new species to the genus (*P. torta* and *P. popla*). Later, he added four more new species to the genus (*P. absona*, *P. darlingtoni* and *P. hackeri* Drake 1952; *P. solla* Drake and Ruhoff 1961).

The genus presently comprises seven Australian species (New South Wales and Queensland) (Drake and Ruhoff 1965). Three new species from New Caledonia are described here. In addition, Drake (1961) described a new genus and a new species from a single specimen caught in New South Wales: *Alloeocysta approba*. This species, the only included species of the ge-

nus, shares with *Parada* the form of the lateral carinae, the paranota and the hood, and is considered a junior synonym. *Alloeocysta approba* Drake is transferred to *Parada*. In addition, *Cysteochila cubens* Guilbert (in press), described from New Caledonia shows affinities with the species of *Parada* and could be an intermediate species between these two genera. Among these relationships, the evolution of some characters getting narrower are discussed through a cladistic analysis. Deposition of types is specified: MNHN for Muséum National d'Histoire Naturelle, Paris; BPBM for Bernice P. Bishop Museum, Hawaii. All measurements are in millimeters.

SYSTEMATICS

Parada Horváth 1925

Cysteochila (Parada) Horváth 1925: 3.

Type species: *Cysteochila (Parada) taeniophora* Horváth 1925: 3, by orig. desig.

Parada: Drake 1942: 4.

Alloeocysta Drake 1961: 109. **New Synonymy.** Type species: *Alloeocysta approba* Drake 1961: 109, by orig. desig.

Diagnosis.—Head with at least two frontal and two occipital spines. Bucculae wide, with apices meeting in front. Antenna long, slender, first segment short, second smallest, third longest and fourth longer than first two together, pubescent.

Pronotum gibbose, deeply punctuate, areolate at apex, pubescent near collar, tricarinate. Median carina long, slightly erected, contiguous to hood. Lateral carinae elevated, ending before collar, curved inward, not resting on pronotum, modified as to form a long inflated areolate cyst. Hood inflated, raised. Paranota long, wide, reflexed upright, not resting on pronotum, three to four areolae broad, almost reaching lateral carinae.

Hemelytra wider and longer than abdomen, slightly wider than pronotum width. Costal area uni- to biseriolate, outer margins bent upward. Subcostal area bi- to triseriate, outer margins bent downward. Discoidal area five to seven areolae broad. Sutural area large, with larger areolae than subcostal and discoidal areas. Hypocostal laminae uniseriate.

Parada approba (Drake), **new combination**
(Figs. 7–8)

Alloeocysta approba Drake 1961: 109.

Comments.—According to Drake (1961) *Alloeocysta approba* is different “from other Australian genera by having the hood distinctly wider than long and the lateral carinae inflated, cyst-like on disc of pronotum” (Holotype measurements, body length 2.99; body width 1.26; hood length 0.37; hood width 0.55). All species of *Parada* have lateral carinae inflated like *A. approba* and some of them have a hood wider than long. This is the case of *P. majuscula* and *P. paitae*. *Alloeocysta approba* has antennae as long as that of the species of *Parada* (I, 0.15: II, 0.12: III, 0.85: IV, 0.3), a pronotum gibbose, deeply punctuate and areolate at apex, a hood forming a vesicle wider than long, lateral carinae modified as to

form a subcylindrical areolate cyst that is closed inward by the internal margins touching the pronotum, while it is not the case for the species of *Parada*. The hemelytra are a little longer than abdomen with a costal area uniseriate, a subcostal area biseriolate and a discoidal area four to five areolae broad. Despite some characters which distinguish *A. approba* from species of *Parada*, *approba* being the unique species of the genus *Alloeocysta*, the latter is considered a synonym of the genus *Parada*. Thus, I propose the new combination *Parada approba* (Drake) **n. comb.**

Type.—Holotype: ♂, Bogan river, New South Wales, Australia (Australian Museum, Sydney).

Parada majuscula Guilbert, **new species**
(Figs. 1–3)

Description.—Head and body black, legs and antenna yellowish to brown fuscous, distal part of fourth antennal segment and tarsi brown to black. Pronotum clear brown to fuscous. Hemelytra yellowish with three dark brown spots, one near base that may occupy just basal third of costal area or be expanded to cover all of the basal third of the hemelytron, plus clear brown spots at apical third and apex of costal area. Length 3.05; width 1.17.

Head with two frontal and two small, slender occipital spines. Bucculae wide, triseriate, with apices meeting in front. Labium reaching hind coxae and labial sulcus sinuate. Sternal laminae widely separated on metasternum. Antennal measurements: I, 0.19: II, 0.12: III, 1.01: IV, 0.45), last antennal segment pubescent.

Pronotum gibbose, deeply punctuate, areolate on hind process, pubescent near collar, tricarinate. Median carina long, slightly elevated, contiguous to hood. Lateral carinae elevated, ending before collar, curved inward, not resting on pronotum, modified as to form a long inflated open cyst, four areolae broad. Hood inflated, raised, slightly wider than long (length 0.33; width 0.38). Paranota long, wide, reflexed and partially

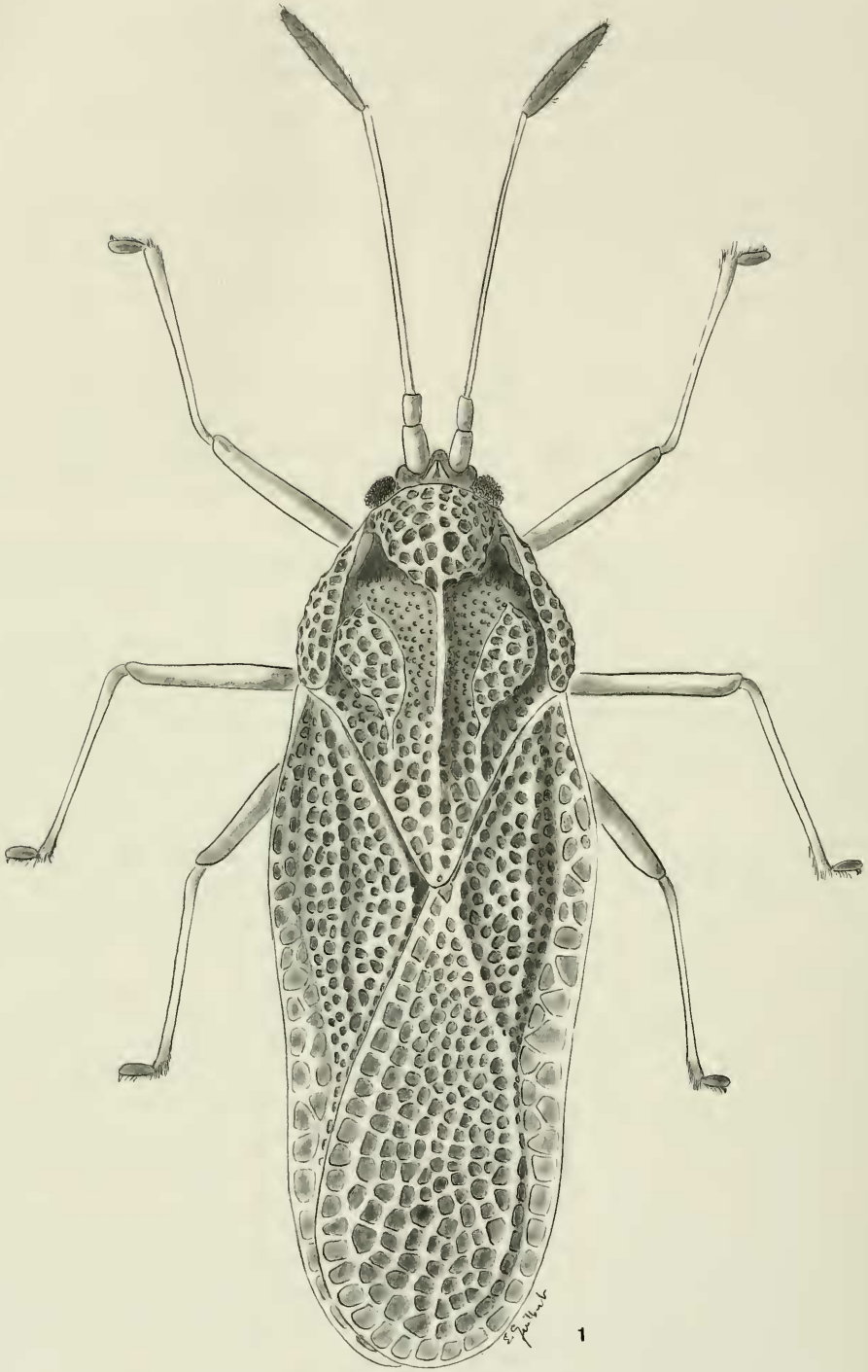
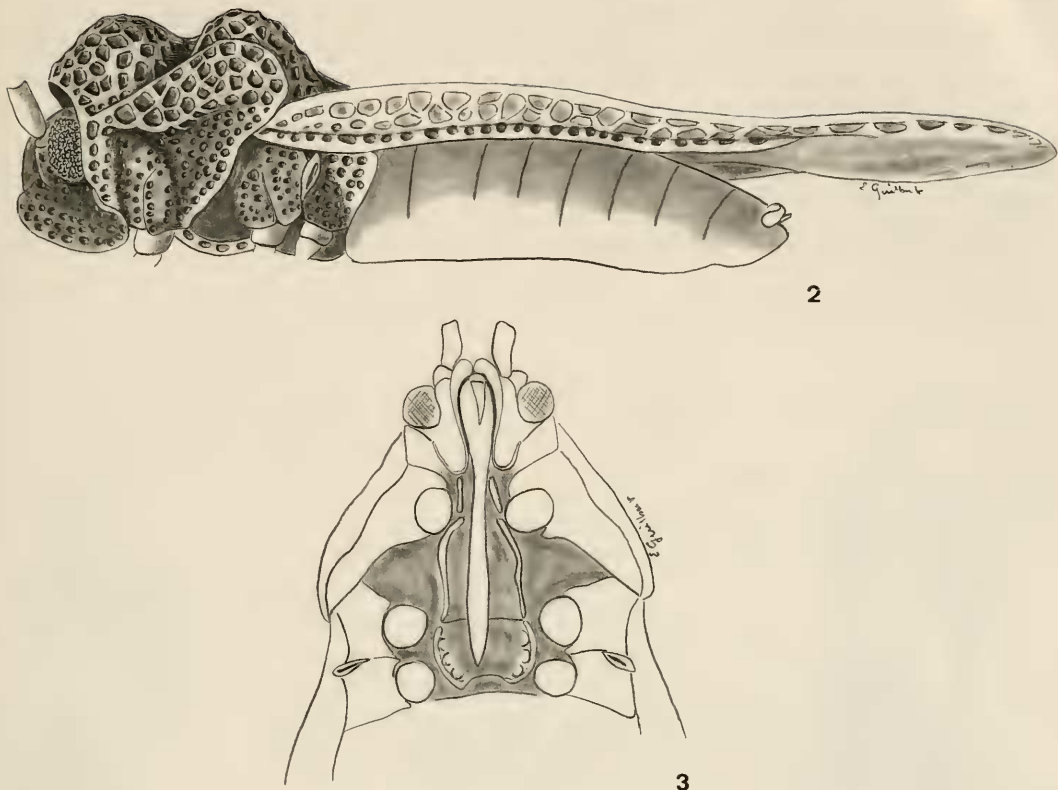


Fig. 1. *Parada majuscula*, habitus. Scale = 1 mm.



Figs. 2-3. *Parada majuscula*. 2, Profile. 3, Ventral face. Scale = 1 mm.

recurved above pronotum, not resting on pronotum, four small areolae broad, almost reaching lateral carinae.

Hemelytra wider, longer than abdomen, slightly wider than pronotum width. Costal area bent upward, mostly biseriate but uniseriate at apex, outer areolae larger than inner. Subcostal area bent downward, triseriate. Discoidal area pentaseriate. Sutural area large, with larger areolae than subcostal and discoidal areas at apex. Hypocostal laminae uniseriate.

Types.—Holotype: ♂, New Caledonia, Rivière Bleue P7, dense evergreen rainforest, 24.X.1992, L. Bonnet de Larbogne, J. Chazeau & E. Guilbert colls (fogging) (MNHN). Paratypes: 1 ♀, same data as holotype (MNHN); 3 ♂ and 1 ♀, New Caledonia, Yahoue III.1978, N.L.H. Krauss coll., Acc. #1978.114 (BPBM); 1 ♀, New Caledonia, 6 km N of Païta, 25.I.1963,

C.M. Yoshimoto coll. (BPBM); 1 ♂, New Caledonia, Mt Koghis, 400–600 m, II.1980, N.L.H. Krauss coll., Acc. #1980.128 (BPBM).

Comments.—The body length of this species may be sexually dimorphic (Table 1), but this characteristic cannot be assessed here because of the small number of specimens.

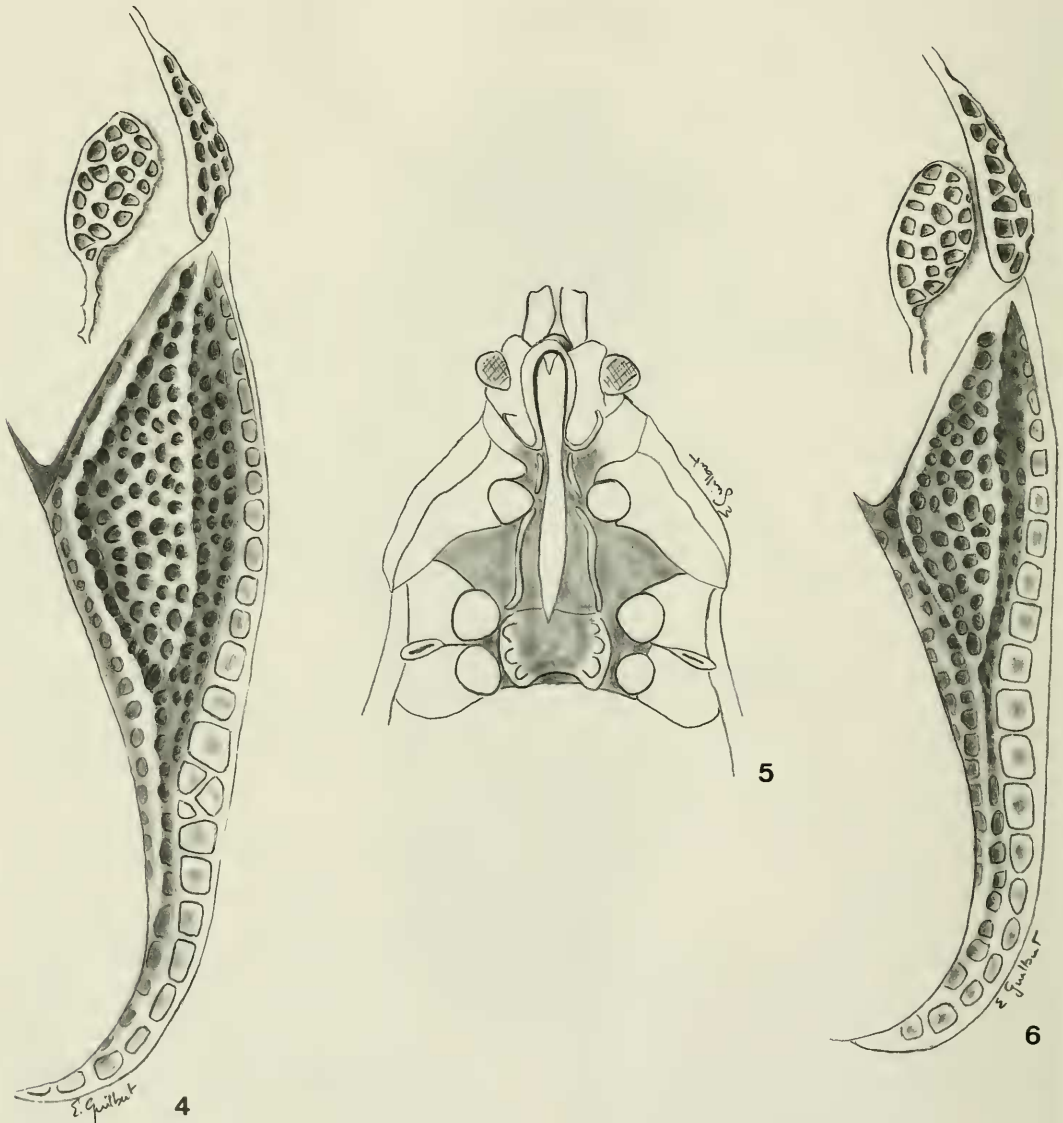
***Parada paitae* Guilbert, new species**
(Figs. 4-5)

Description.—Head and body brown. Pronotum, hemelytra, legs and antenna clear to yellowish, apex of last antennal segment brown fuscous. Length 2.98; width 1.17; hood length 0.31; hood width 0.31.

Same characters as *P. majuscula*, except rostrum extends between median coxae but does not reach hind coxae, costal area is uniseriate, areolae are rather large, except

Table 1. Means of body, hood and antennal segments measurements for 5 males and 3 females of *P. majuscula* in mm.

	Body		Hood		Antennal Segments			
	Length	Width	Length	Width	I	II	III	IV
Males	2.991	1.102	0.32	0.372	1.003	0.366	0.191	0.123
Females	3.149	1.272	0.349	0.400	1.010	0.292	0.200	0.123
Both	3.05	1.165	0.331	0.383	1.006	0.451	0.194	0.123



Figs. 4-6. *Parada* spp. 4, *P. paitae*, right hemelytra, paranota and lateral carina of the habitus. 5, *P. paitae*, ventral face. 6, *P. minuta*, right hemelytra, paranota and lateral carina of the habitus. Scale = 1 mm.

Table 2. Body length, body width, hood length, hood width and antennal segments measurements of the New Caledonian species and *P. approba*. Last antennal segment measurements on *P. approba* is missing on the type.

Species	Body		Hood		Antennal Segments			
	Length	Width	Length	Width	I	II	III	IV
<i>Parada majuscula</i>	3.05	1.17	0.33	0.38	0.19	0.12	1.01	0.45
<i>Parada paitae</i>	2.98	1.17	0.31	0.31	0.17	0.12	0.94	0.40
<i>Parada minuta</i>	2.63	0.94	0.29	0.31	0.15	0.11	0.92	0.43
<i>Parada approba</i>	2.99	1.26	0.37	0.55	0.15	0.12	0.85	—

one or two areolae divided into two areolae at level of apex, and discoidal area five to six areolae broad. Antennal segments measurements: I, 0.17: II, 0.12: III, 0.94: IV, 0.40.

Types.—Holotype: ♀, New Caledonia, Mont Nondoué near Païta, sclerophyllous forest, 16.X.1992, L. Bonnet de Larbogne, J. Chazeau & E. Guilbert colls (fogging) (MNHN). Paratype: 1 ♀, New Caledonia, Mont Nondoué near Païta, sclerophyllous forest, 28.IV.1993, L. Bonnet de Larbogne, J. Chazeau & E. Guilbert colls (fogging) (MNHN).

***Parada minuta* Guilbert, new species**
(Fig. 6)

Description.—Head and pronotum brown, body, hemelytra, legs and antenna clear to yellowish, last antennal segment brown fuscous, some brown spots on hemelytra on discoidal and sutural areas. Length 2.63; width 0.94; hood length 0.29; hood width 0.31.

Head short, with four tiny spines. Antennal segments as two former species. Antennal segments measurements: I, 0.15: II, 0.11: III, 0.92: IV, 0.43. Bucculae short, wide, three areolae broad. Labium short, not extending beyond mesosternum, labial sulcus widened between hind coxae.

Pronotum gibbose, areolate, tricarinate, median carina uniseriate, elevated, lateral carinae wide, four areolae broad. Paranota four areolae broad.

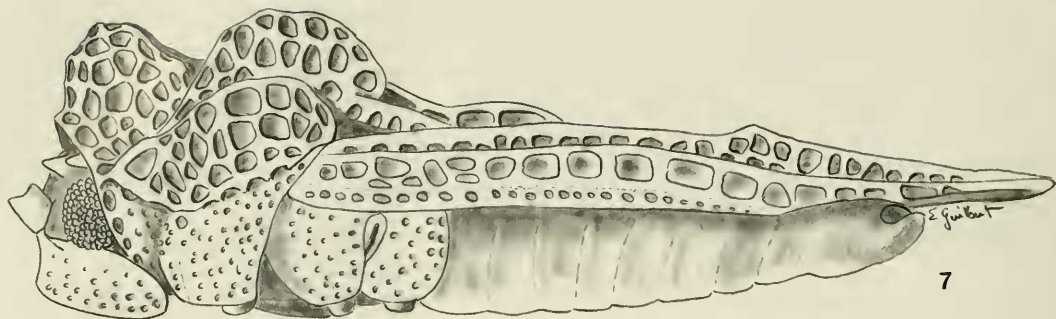
Costal area completely uniseriate, subcostal area biseriate, discoidal area short,

half length of hemelytra, five areolae broad at widest part.

Types.—Holotype: ♂, New Caledonia, Ile des Pins: Vao, 0–100 m, I. 1985, N.L.H. Krauss coll. (BPBM). Paratype: 1 ♂, same data as the holotype (BPBM).

KEY TO SPECIES OF *PARADA*

1. Head armed with 4 cephalic spines 2
- Head armed with 5 cephalic spines 4
2. Subcostal area triseriate at widest part 3
- Subcostal area biseriate at widest part (Fig. 6) *P. minuta* Guilbert, n. sp.
3. Labium extending beyond hind coxae (Fig. 3) *P. majuscula* Guilbert, n. sp.
- Labium not reaching hind coxae (Fig. 5) *P. paitae* Guilbert, n. sp.
4. Paranota three areolae wide 5
- Paranota four areolae wide 6
5. Median carina areolate and uniseriate (Fig. 15) *P. solla* Drake and Ruhoff
- Median carina not areolate *P. taeniophora* (Horváth)
6. Lateral carinae five areolae wide (Fig. 10) *P. absona* Drake
- Lateral carinae less than five areolae wide 7
7. Third antennal segment 4 times longer than last *P. approba* (Drake)
- Third antennal segment less than 4 times longer than last 8
8. Costal area with areolae the same size than that of subcostal area (Fig. 12) *P. hackeri* Drake
- Costal area with areolae larger than that of subcostal area 9
9. Lateral carinae width of 2 areolae broad (Fig. 14) *P. darlingtoni* Drake
- Lateral carinae width of 3 areolae broad 10
10. Costal area largely biseriate at base (Fig. 9) *P. popla* Drake
- Costal area uniseriate except for two areolae across very base (Fig. 11) *P. torta* Drake



7



8

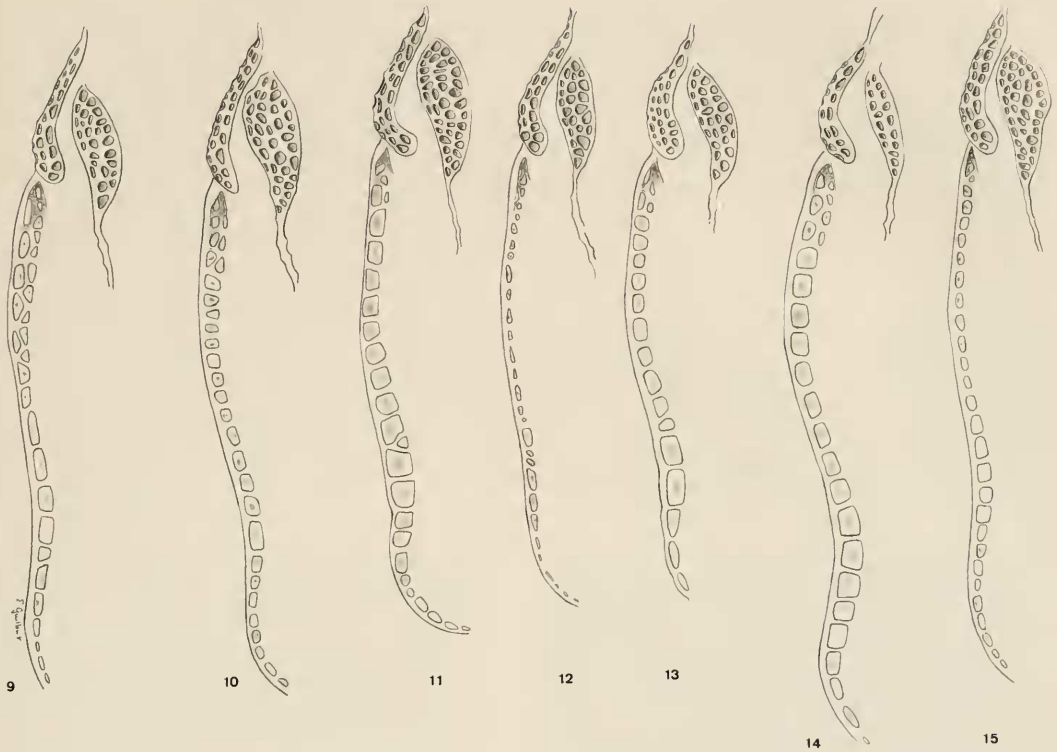
Figs. 7-8. *Parada approba*. 7, Profile. 8, Ventral face. Scale = 1 mm.

CLADISTIC ANALYSIS

Choice of the taxa.—The eleven species of the genus *Parada* are included in this analysis as the ingroup. Three species are included as outgroups: *Cystechila cubens* Guilbert, *Physatocheila dissimilis* Guilbert and *Nobarnus pilosus* Guilbert. *Cystechila cubens* shows some affinities with the genus *Parada*, while *N. pilosus* is clearly different. *Physatocheila dissimilis* could be considered as intermediate between these two genera by its general morphology. Therefore, 14 species were included in this analysis.

Character states.—Sixty-one morphological characters are analysed. They are analysed in two different ways. A first analysis concern all the characters. A second analysis concern only fifty-one characters

active and ten inactive. These ten characters define the size of various structures in terms of number of areolae. They are not used in the analysis because the homology between the areolae cannot be established with certainty, but they figure as attributes. When a structure has two areolae, does it mean that an areola divided into two areolae, or does a second areola appears near the existing one? The results of the two analyses are compared. Inactive characters in the second analysis are mentioned. Characters of the genitalia are not taken into account because they do not vary within the genus. Multi-state characters are treated unordered. The matrix of characters is given in Table 3. Question marks represent characters lacking or uncertainly stated.



Figs. 9–15. *Parada* spp. left costal area, paranota and lateral carinae. 9, *P. popla*. 10, *P. absona*. 11, *P. torta*. 12, *P. hackeri*. 13, *P. taeniophora*. 14, *P. darlingtoni*. 15, *P. solla*. Scale = 1 mm.

- | | |
|--|--|
| 0. Head black (0), brown (1), yellowish to white (2). | 12. Occipital spines stout (0), slender (1). |
| 1. Pronotum black (0), brown (1), yellowish (2). | 13. Median spine long (0), short (1), tubercle-like (2), absent (3). |
| 2. Abdomen black (0), brown (1), yellowish (2). | 14. Median spine erect (0), prostrate (1). |
| 3. Hemelytra black (0), brown (1), yellowish to white (2), brown with colored spots (3). | 15. Median spine stout (0), slender (1). |
| 4. Body glabrous (0), pilose (1). | 16. Antennae densely pubescent (0), not pubescent (1). |
| 5. Head convex (0), flat (1). | 17. Last antennal segment longer than first and second together (0), shorter than first and second together (1). |
| 6. Frontal spines long (0), short (1). | 18. Last antennal segment longer than first (0), shorter than first (1). |
| 7. Frontal spines erect (0), prostrate (1). | 19. Third antennal segment 1 time as long as the last one (0), 2 times (1), 3 times (2), 4 times (3). |
| 8. Frontal spines stout (0), slender (1). | 20. Bucculae biseriate (0), triseriate (1), quadriseriate (2), pentaseriate (3). Inactive character. |
| 9. Frontal spines in contact or crossed (0), not in contact (1). | 21. Bucculae open in front (0), closed in front (1). |
| 10. Occipital spines long (0), short (1). | 22. Labium almost extending beyond the |
| 11. Occipital spines adpressed (0), prostrate (1). The occipital spines are prostrate when the spines do not rest onto the head, otherwise they are adpressed. | |

Table 3. Matrix of states of the 61 characters for 14 species.

Taxa	Character states
<i>Nobarnus pilosus</i>	00001100000003??01111012100100?00?01??0004200010010030??202133
<i>Physatocheila dissimilis</i>	01110100000100001102101110101210?01??0111101111111001??110420
<i>Cystocheila cubens</i>	222300011000120?1?02212001010?305112?03200111111110102010512
<i>Parada darlingtoni</i>	101300001000101110021110?001121122032111411110110112110111220
<i>Parada hackeri</i>	11130101000001111001014010111221211?111311110110110110111110
<i>Parada torta</i>	1012001110001111100221101001102142121111411110110112100111120
<i>Parada absona</i>	00030001110011111002111000011221521101112111111011110111220
<i>Parada popla</i>	0013001110001111100211300001122132042111411110110111120111320
<i>Parada solla</i>	111301011000111110021120100111216212112131111110111100111221
<i>Parada taeniophora</i>	10130011100011011??211111001112122021121311110110112110111120
<i>Parada majuscula</i>	01030011101013??10012101010111210213212131111110111122111111
<i>Parada paitae</i>	11110011111013??10011121000112211211112141111110111101111221
<i>Parada minuta</i>	22230011101013??10011131000112210211112131111110111100111120
<i>Parada approba</i>	101300011?00?00?100311310101??2122142111411110110111110111020

- metasternum (0), extending to the middle of the metasternum (1), extending little beyond the mesosternum (2), reaching the posterior margins of the mesosternum (3), extending to the middle of the mesosternum (4).
23. Mesosternal laminae subparallel (0), not subparallel (1).
24. Metasternal laminae wide (0), narrow (1).
25. Sternal laminae open behind (0), closed behind (1).
26. Pronotum strongly gibbose (0), slightly gibbose (1).
27. Pronotum pubescent (0), glabrous (1).
28. Median carina not areolate (0), uniseriate (1).
29. Median carina with large areolae (0), small areolae (1), minute areolae (2).
30. Lateral carinae ridge like (0), with one or two rows of areolae (1), with 3 to 5 rows of areolae (2), with 6 or more than 6 rows of areolae (3). Inactive character.
31. Lateral carinae erect (0), reflexed but not resting onto the pronotum (1), reflexed and resting onto the pronotum (2).
32. Lateral carinae 8 areolae long (0), 9 areolae long (1), 10 areolae long (2), 11 areolae long (3), 12 areolae long (4), 14 areolae long (5), 15 areolae long (6). Inactive character.
33. Hood absent (0), present but flat (1), cyst-like and partly covering the head (2). When the hood is present, it covers most of the head but generally not the eyes.
34. Hood higher than posterior pronotal lobe (0), not higher than posterior pronotal lobe (1).
35. Hood 3 areolae long (0), 4 areolae long (1), 5 areolae long (2), 6 areolae long (3), 7 areolae long (4). Inactive character.
36. Hood 1 areola high (0), 2 areolae high (1), 3 areolae high (2). Inactive character.
37. Collar triseriate (0), biseriate (1). Inactive character.
38. Paranota 2 areolae broad (0), 3 areolae broad (1), 4 areolae broad (2), 5 areolae broad (3). Inactive character.
39. Paranota with large areolae (0), small areolae (1), minute areolae (2).
40. Paranota more than 14 areolae long (0), 13–14 areolae long (1), 11–12 areolae long (2), 10 areolae long (3), 8–9 areolae long (4). Inactive character.
41. Paranota reflexed with free margins in contact with pronotum (0), reflexed with free margins not in contact with

- pronotum (1), not reflexed with free margins not in contact with pronotum (2).
42. Paranota not covering pronotum (0), covering part of pronotum (1).
 43. Hemelytra wide (0), narrow (1). Hemelytra are considered narrow when not extending far beyond the abdomen.
 44. Hemelytra sharply widened at base (0), not sharply widened at base (1).
 45. Junction of RM and Cu veins raised and forming a little swollen zone (0), not raised and forming a little swollen zone (1).
 46. Hemelytra areolae hyaline (0), not hyaline (1).
 47. Hemelytra pubescent (0), glabrous (1).
 48. Hemelytral veins raised, forming ridges (0), not raised and forming ridges (1).
 49. Costal area wide (0), narrow (1).
 50. Costal area plane (0), raised (1).
 51. Costal area areolae very small (0), small (1), large (2), very large (3).
 52. Costal area 6 areolae broad (0), uniseriate (1).
 53. Costal area uniseriate at base (0), biseriata at base along 3–5 areolae (1), biseriata at base along 7–10 areolae (2). The costal area is mostly uniseriate and shows in part two areolae for the same width like if the original areolae were divided in two smaller areolae (Figs. 9–15).
 54. Costal area uniseriate at the middle (0), biseriata at the middle along 2–3 areolae (1), biseriata at the middle along 5–6 areolae (2).
 55. Subcostal area areolae very small (0), small (1), large (2), very large (3).
 56. Subcostal area large (0), small (1).
 57. Discoidal area areolae very small (0), small (1), large (2), very large (3).
 58. Discoidal area 4 areolae wide (0), 5 areolae wide (1), 6 areolae wide (2), 7 areolae wide (3), 8 areolae wide (4), 9 areolae wide (5). Inactive character.
 59. Sutural area areolae very small (0), small (1), large (2), very large (3).
 60. Sutural area 6–7 areolae wide (0), 8–9

areolae wide (1), 12 areolae wide (2), less than 6 areolae wide (3). Inactive character.

The phylogenetic analysis was performed with Hennig86 (Farris 1988). The algorithm *ie** was used to build tree (s), using Fitch parsimony.

RESULTS

First analysis.—Three trees of 119 steps, with *ci* = 61 and *ri* = 50 were generated. They differ by the relative position of the three New Caledonian species among themselves. Seventy-seven percent of the active characters are not informative for the resolution of these conflicting branches. Here is presented one of the trees which corresponds to the following interpretation (Fig. 16). For the 7 informative characters, *Parada minuta* and *P. paitae* share the same state for four of them, while *P. majuscula* and *P. minuta* share the same state for one of them, and *P. majuscula* and *P. paitae* for any of them. Then, *Parada minuta* may be more closely related to *P. paitae* than to *P. majuscula*. The coefficients and number of steps for each characters is given Table 4.

The genus *Parada* (including the species *approba*) is monophyletic. The monophyly of the genus is supported by the raised veins on the hemelytra, the lateral carinae and the paranota which are curved inwards but not resting onto the pronotum.

The genus is divided in two groups, the New Caledonian group which comprise the three New Caledonian species, and the Australian group comprising the other eight species. The Australian species have five cephalic spines, while New Caledonian species have four. No unambiguous synapomorphy support the monophyly of the Australian group, while the short occipital spine and the lack of a median spine are the unambiguous synapomorphies of the New Caledonian group. *Parada approba* is completely integrated in the genus; however, it is the basal species

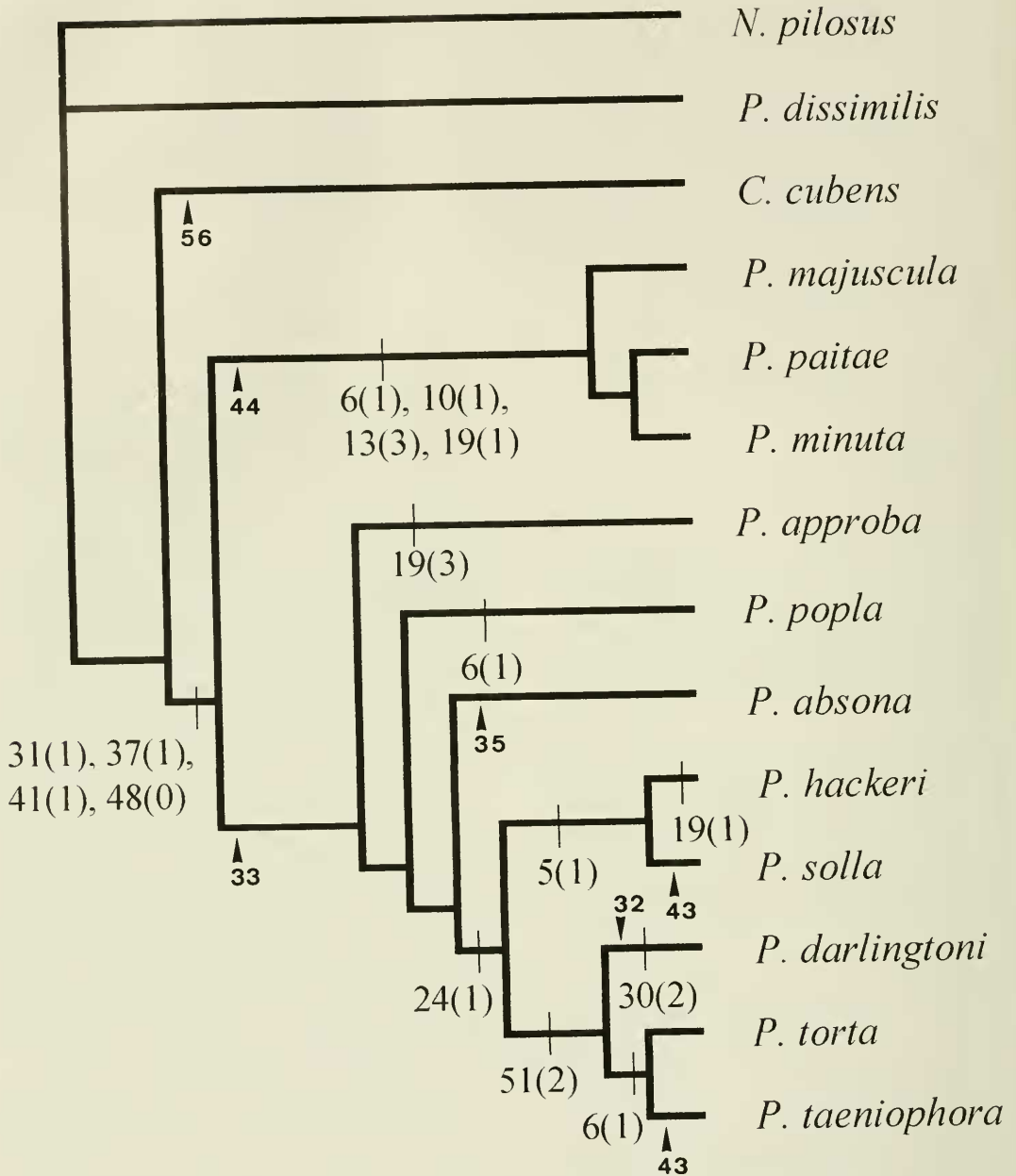


Fig. 16. One of the three cladograms obtained with the *ic** command of Hennig86 on data show in table 3 (14 taxa, 61 active characters). Length = 119 steps, *ci* = 61, *ri* = 50. Paranota and lateral carinae width, respectively, in number of areolae are indicated under an arrow on the cladogram.

of the Australian group. It is characterised by the third antennal segment that is four times the length of the last. *Parada popla*, *P. absona* and *P. approba* are the basal species of the Australian group. They

have a labial sulcus broad like the New Caledonian species. Among the Australian group, two subgroups can be distinguished, the *hackeri* subgroup composed by *P. hackeri* and *P. solla*, and the *dar-*

Table 4. Number of steps, ci and ri for each character for the first analysis (10 characters inactive) and the second analysis (all characters active).

Char-acters	Analysis 1			Analysis 1		
	Steps	ci	ri	Steps	ci	ri
1	5	40	40	5	40	40
2	5	40	40	5	40	40
3	5	40	0	5	40	0
4	4	75	0	4	75	0
5	1	100	100	1	100	100
6	2	50	66	3	33	33
7	3	33	60	3	33	60
8	2	50	50	2	50	50
9	2	50	50	2	50	50
10	2	50	0	2	50	0
11	1	100	100	1	100	100
12	1	100	100	1	100	100
13	2	50	50	2	50	50
14	5	60	60	5	60	60
15	2	50	66	3	33	33
16	1	100	100	1	100	100
17	1	100	100	1	100	100
18	1	100	100	1	100	100
19	1	100	100	1	100	100
20	4	50	50	4	50	50
21	5	40	0	5	40	0
22	1	100	100	1	100	100
23	7	57	40	8	50	20
24	3	33	66	3	33	66
25	2	50	75	4	25	25
26	3	33	0	3	33	0
27	2	50	50	2	50	50
28	1	100	100	1	100	100
29	2	50	0	2	50	0
30	4	50	0	3	66	50
31	4	75	0	4	75	0
32	1	100	100	1	100	100
33	7	85	50	7	85	50
34	3	66	50	2	100	100
35	2	50	0	2	50	0
36	7	42	0	6	50	25
37	5	40	0	3	66	66
38	1	100	100	1	100	100
39	5	60	50	3	100	100
40	2	100	100	2	100	100
41	7	57	25	6	66	50
42	2	100	100	2	100	100
43	1	100	100	1	100	100
44	1	100	100	1	100	100
45	1	100	100	1	100	100
46	4	25	25	3	33	50
47	1	100	100	1	100	100
48	1	100	100	1	100	100
49	1	100	100	1	100	100
50	1	100	100	1	100	100
51	1	100	100	1	100	100

Table 4. Continued.

Char-acters	Analysis 1			Analysis 1		
	Steps	ci	ri	Steps	ci	ri
52	4	75	75	5	60	50
53	1	100	100	1	100	100
54	5	40	25	4	50	50
55	3	66	0	3	66	0
56	2	100	100	2	100	100
57	1	100	100	1	100	100
58	2	100	100	2	100	100
59	9	55	0	8	62	25
60	4	50	0	4	50	0
61	5	60	33	4	75	66

lingtoni subgroup composed by *P. darlingtoni*, *P. torta* and *P. taeniophora*. The monophyly of both subgroups together is supported by a narrow labial sulcus. The monophyly of *hackeri* subgroup is supported by a flat hood. The monophyly of *darlingtoni* subgroup is supported by very large areolae on costal area. The slightly gibbose pronotum is autapomorphic for *P. hackeri*, and the large areolae of the median carina is autapomorphic for *P. torta*.

Second analysis.—A single tree of 168 steps, with ci = 62 and ri = 48 is generated (Fig. 17). The conflicting branch between the New Caledonian species is resolved, and *Parada minuta* is more closely related to *P. paitae* than to *P. majuscula*. As in the first analysis, the genus *Parada* is monophyletic. The monophyly being supported by the same characteristics. *Parada hackeri* is the basal species of the genus. It is the only species of *Parada* with stout frontal and occipital spines, biseriate bucculae and having the shortest rostrum of the genus. It shares the same hood shape and the same size of areolae on costal area than *Cysteochila cubensis*, the outgroup most related to the genus. The other species of the genus is divided in two groups, the *torta* group, comprising *P. torta* (basal species of the group), *P. absona*, *P. popla*, *P. darlingtoni* and *P. approba*, and the *solla* group, comprising *P. solla* (basal species of the

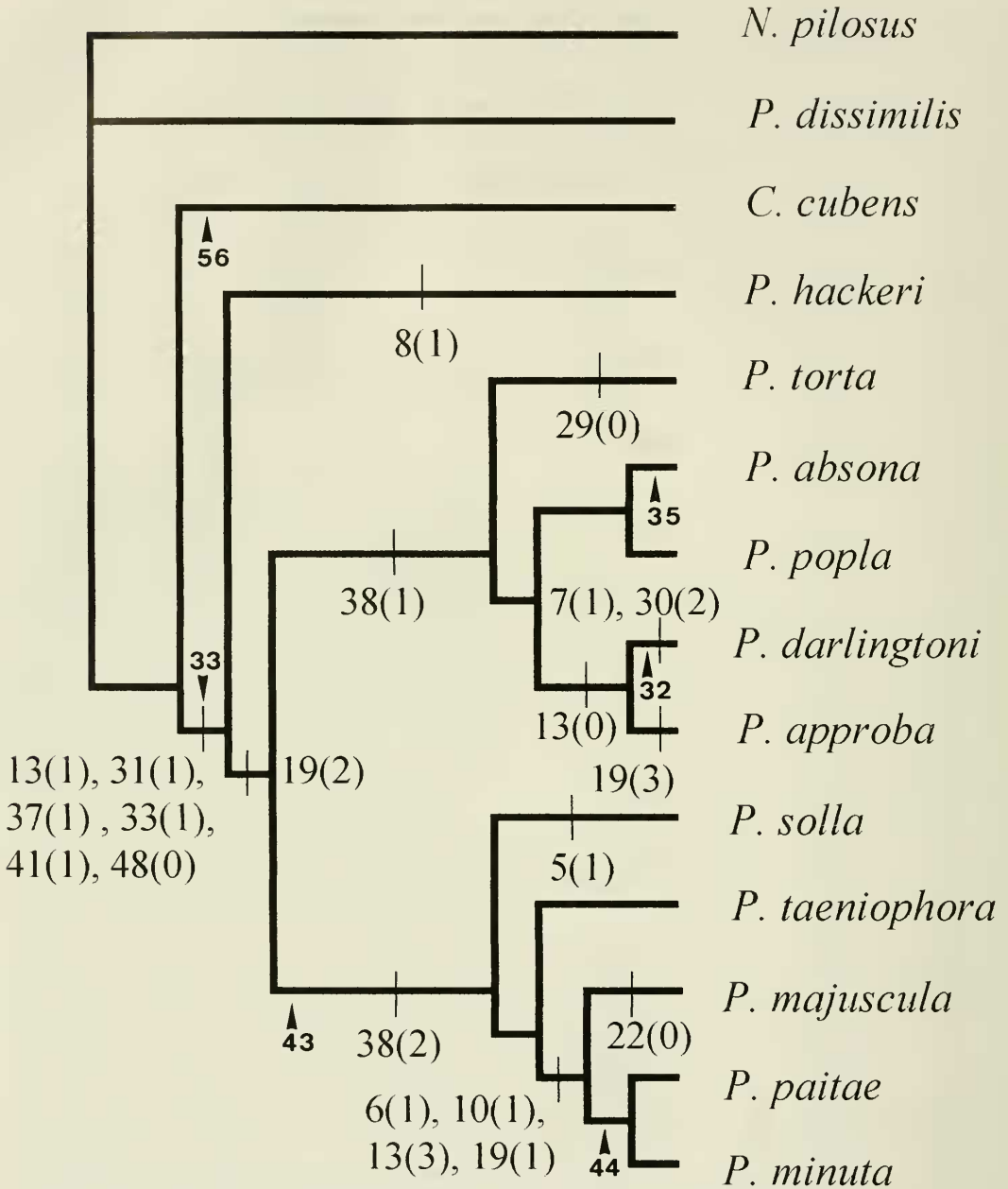


Fig. 17. The single three cladograms obtained with the *ic** command of Hennig86 on data show in table 3 (14 taxa, 51 active characters). Length = 168 steps, *ci* = 62, *ri* = 48. Paranota and lateral carinae width, respectively, in number of areolae are indicated under an arrow on the cladogram.

group), *P. taeniophora*, *P. majuscula*, *P. paitae* and *P. minuta*. The *torta* group is characterized by the paranota three areolae wide, that is shared with *Parada hackeri* and the outgroup *Physatocheila dissi-*

milis. The *solla* group is characterized by the paranota four areolae wide, the only autapomorphic character for the group. The coefficients and number of steps vary for 15 characters over 61 between the two

analysis (Table 4), 6 of them being inactive in the first one.

DISCUSSION AND CONCLUSION

The species of *Parada* can easily be recognized by the combination of the paranota (characters 41, 42), the lateral carinae (characters 30, 31) and the costal area shapes (characters 49 to 54).

Despite the different results of the two analyses, some characters have the same tendencies of evolution. The lateral carinae and the paranota width in terms of number of areolae used as attributes in the first analysis (because of their uncertain homologies) narrow from basal to terminal taxa. However, these tendencies in the second analysis are not as clear as in the first one.

In the first analysis, the width of the lateral carinae narrow from the outgroup *C. cubens* (lateral carinae 6 areolae broad) to the New Caledonian group (4 areolae broad), the Australian group (3 areolae broad) and *P. darlingtoni* (2 areolae broad), except for *P. absona* which has lateral carinae of 5 areolae broad (Figs. 9–15). The same way, the paranota narrow from *C. cubens* (5 areolae broad) to the New Caledonian group (4 areolae broad) and the Australian group (3 areolae broad). There are two reversals for *P. solla* and *P. taeniphora* which have the paranota 4 areolae broad. The others pronotal and hemelytral characters do not show such a tendency. However, the lateral carinae and the paranota are longer in terms of number of areolae for *C. cubens* than for the *Parada* species, and the lateral carinae of the New Caledonian species is shorter than the one for the Australian species.

In the second analysis, the lateral carinae narrow from *C. cubens* to *Parada* species from 6 to 3 areolae wide. They still narrow in the torta group for *P. darlingtoni* from 3 to 2 areolae wide, while they enlarge in the *solla* group for the three New Caledonian species from 3 to 4 areolae. There is also a reversion for *P. absona* which lateral carinae enlarge to 5 areolae wide. The paranota

narrow from *C. cubens* to *Parada* species from 5 to 3 areolae wide but enlarge in the *solla* group to 4 areolae.

If characters such as the width among the different hemelytral areas and the various pronotal expansions like the hood, the lateral carinae and the paranota show a trend of evolution, this is not the case of other characters such as the length of the lateral carinae and the paranota. They do not show any extension or shortening through the cladogram. Thus, wide lateral carinae and wide paranota could be plesiomorphic. The two major groups found by the first analysis, are separated by a geographic barrier: the sea between the Queensland and New Caledonia, isolated from Australia since the Triassic. Then, lateral carinae and paranota still narrowed in Australia after the Triassic. However, these characters show slight variation among *Parada* species, in comparison with other genera. As a general rule, Tingidae present traits that have no apparent biological explanation and that could be hypertelic by their disproportionate size. But, these possibilities still require further study and much more data such as behavioral parameters, and host plants, need to be added to test these evolutionary hypotheses.

ACKNOWLEDGMENTS

I am most grateful to Gordon Nishida (B. P. Bishop Museum, Honolulu, Hawaii) for the loan of many specimens, and Thomas Henry (Systematic Entomology Laboratory, USDA) for his helpful support in the access to the types at the National Museum of Natural History, Smithsonian Institution, Washington, DC. I am also indebted to Cyril d'Haese, Philippe Grandcolas, Laure Desutter-Grandcolas, and Thierry Bourgoin (MNHN, Paris) for their fruitful comments.

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